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Lovett, J.C. (1999) Tanzanian forest tree plot diversity and elevation. *Journal of Tropical Ecology*. pp. 689-694. ISSN 1469-7831

<https://doi.org/10.1017/S0266467499001108>

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SHORT COMMUNICATION

Tanzanian forest tree plot diversity and elevation

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KEY WORDS: Diversity, elevation, Tanzania, forest, trees

Observed variation in species richness on ecological gradients and between regions has attracted several different explanations. Climatic factors, such as energy availability, precipitation and mean annual temperature, are frequently cited to explain differences in species richness (Wright *et al.* 1993). The relative amount of variation in these variables may be of importance as well as absolute values (Stevens 1989, 1992). Alternatively, the history of colonization and extirpation have been used to explain regional variation in diversity (Guo *et al.* 1998; Latham & Ricklefs 1993a, b). Area is an important factor, for example on an elevational gradient the tops of mountains are not only cooler than the bottoms, but they are also much smaller (Rahbek 1997).

In tropical Africa declines in forest tree species richness with elevation have been reported in both fixed area plots and elevational bands (reviewed in Hamilton 1989). However, a study in the Eastern Arc forests of Tanzania using plots in which a fixed number of stems were enumerated (200 plots each of 20 trees of ≥ 20 cm dbh) did not show a decline in species richness of the plots with elevation (Lovett 1996). In this paper additional data (a further 163 plots) are used to confirm this observation and to demonstrate that the number of species found in a plot is independent of the potential pool of species. Examination of some of the plots that are known to be from old secondary forests shows that disturbance may be a factor that leads to low diversity.

A total of 363 plots from the Eastern Arc forests were available for analysis from published and unpublished sources for the following mountains (Table 1): West Usambara (Lovett 1996, Hall 1991); East Usambara (Hamilton *et al.* 1989); Southern Nguru (Lovett 1996); Malundwe (Lovett & Norton 1989); Northern Udzungwa (Lovett 1996); and Southern Udzungwa (Lovett *et al.* 1997,

Table 1. Eastern Arc mountains (with approximate latitude and longitude) where plots were enumerated with number of plots, mean number of species per plot with standard deviation and elevation range of the plots.

Mountain	Number of plots	Mean species per plot	Plot elevation range (m)
West Usambara (4–5°S 38°E)	166	8.9 ± 2.2	1000–2180
East Usambara (4–5°S 38°E)	70	9.5 ± 2.4	280–1220
Southern Nguru (6°S 37°E)	29	10.5 ± 2.2	880–1560
Malundwe (7°S 37°E)	5	11.4 ± 1.7	1120–1155
Northern Udzungwa (7°S 36°E)	78	9.3 ± 2.6	410–1670
Southern Udzungwa (8°S 35°E)	15	7.7 ± 3.5	550–1870

J. Lovett unpubl. data). The Eastern Arc mountains of eastern Tanzania and southeastern Kenya are defined as those mountains on ancient crystalline gneissic rocks under the direct climatic influence of the Indian Ocean from the Makambako Gap (8°51'S 34°49'E) to the Taita Hills (3°25'S 38°20'E) (Lovett 1990). The Eastern Arc forests are unusual in that they contain a high proportion of restricted range species, leading them to be regarded as an important biodiversity 'hotspot' (Mittermeier et al. 1998, Myers 1990). This feature of the forests has been attributed to an exceptionally long period of environmental stability in the area (Lovett & Friis 1996).

The plots were assessed using the twenty-tree variable-area plotless technique (Hall 1991) in which the nearest 20 trees of ≥ 20 cm diameter at breast height (dbh) to an objectively chosen point were measured and identified. Most of the plots were enumerated in moist forest on the eastern slopes with a mean annual rainfall in excess of 1000 mm, the exception being plots from the distinctive dry montane *Juniperus* forests with a rainfall of 600–900 mm y^{-1} from the western West Usambara mountains. There are few meteorological stations in the forested area so it is not possible to directly correlate plot diversity with rainfall. Data from the CIAT/FAO climate database show that rainfall for stations in eastern ($\geq 35^\circ$ E) Tanzania receiving ≥ 1000 mm y^{-1} is not correlated with elevation ($n = 167$, elevation range 0–1921 m, $r^2 = 0.015$, $P = 0.11$). Temperature is correlated with elevation. Eastern Tanzanian meteorological stations receiving ≥ 1000 mm y^{-1} show a lapse rate of 0.5–0.6 °C per 100 m elevation (mean monthly maximum temperature = $-0.50x + 28.55$, $r^2 = 0.96$; mean monthly minimum temperature = $-0.57x + 24.32$, $r^2 = 0.96$; where $x = (\text{m})/100$ elevation).

The potential pool of species that might occur in the plots varies with elevation and rainfall. The Eastern Arc contains a total of 272 forest tree species (67 of which are endemic) that reach ≥ 20 cm dbh (Lovett 1993 gives a figure of 274 species ≥ 20 cm dbh or 10 m tall, but this includes two tall but slender bamboos which would not be enumerated in the 20-tree plots). Because there is a rapid turnover of species with change in elevation (Lovett 1996, 1998), then the number of species that might be included in a plot at any given altitude is substantially less than the total. In Eastern Arc dry lowland forest (0–800 m elevation) there are 52 species, in lowland forest (0–800 m) there

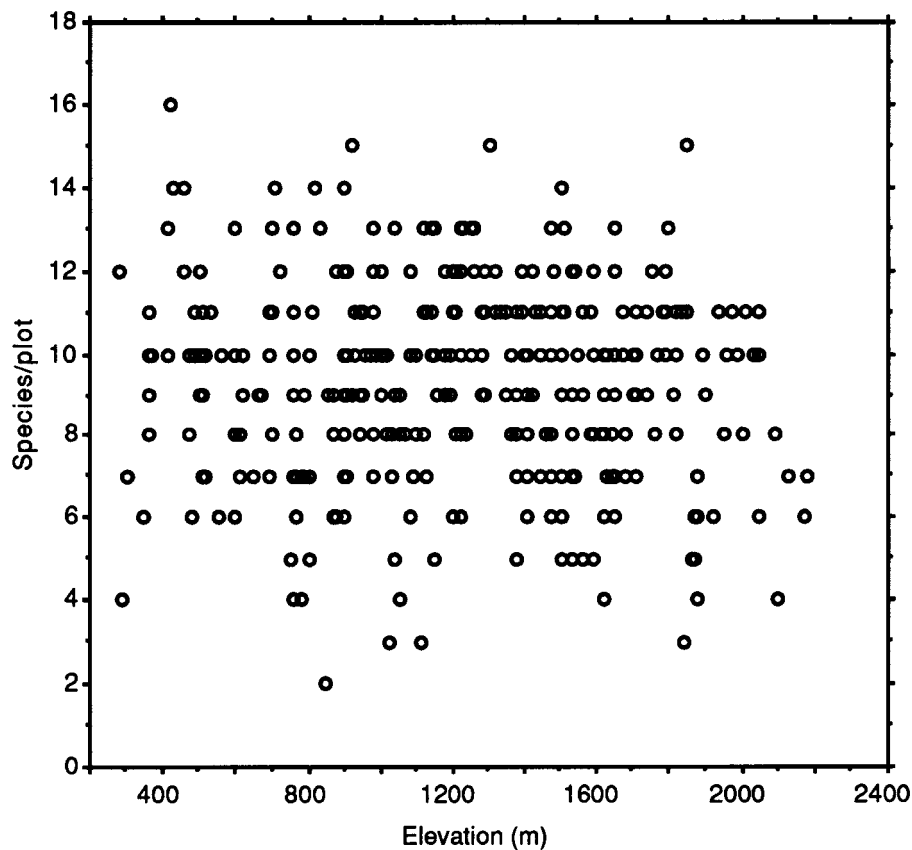


Figure 1. Relationship of number of species in each 20-tree plot and elevation ($n = 363$).

are 91 species, in submontane forest (800–1400 m) there are 114 species, in montane forest (1200–1800 m) there are 120 species, in dry montane forest (1500–2400 m) there are 57 species and in upper montane forest (1800–2400 m) there are 42 species (forest definitions from Lovett 1993).

For the aggregated plot data from the 363 plots the lowest number of species found in a plot was two, and the highest was 16. The mean number of species/plot is 9.2 ± 2.4 , the mode 10 and the median 9. The species richness data is normally distributed with a kurtosis of -0.21 (Kolmogorov–Smirnov normality test $D = 0.026$, $P > 0.15$). The distribution is slightly skewed towards lower species numbers (skewness -0.16). There is a slight negative correlation between the number of species in each plot and elevation (Figure 1, $r^2 = 0.011$, $P = 0.046$). Richness appears to be independent of the potential pool of species. An average plot with nine species contains at least 7.5% of the total species pool at any elevation. Although the species pool is larger at mid-elevations, plot diversity remains constant throughout the elevation range. For example, a species rich upper montane forest plot with 15 species contains 36% of the total species pool in a 20-tree sample.

If the five plots from the driest and structurally different forest type, the montane *Juniperus* forest of the West Usambara mountains (mean species per plot = 5 ± 1.6 , elevation 1840–1880 m, Lovett 1996), are removed from the pool to leave only moist forest plots, then there is no significant correlation between plot species richness and elevation ($n = 357$, $r^2 = 0.005$, $P = 0.17$). The mean rises to 9.3 ± 2.4 , the mode stays at 10 and the median rises to 10. The kurtosis also falls to -0.19 and the skewness to -0.15 . The *Juniperus* forest plots are significantly less diverse than the other plots (two-tailed t-test $P < 0.0001$).

Anthropic disturbance for cultivation is associated with low species richness. Three low diversity plots from the Southern Udzungwa mountains at around 750–1025 m elevation in the Kihansi Gorge are dominated by *Filicium decipiens* (Wight & Arn.) Thw. (Sapindaceae), a tree that occurs throughout eastern Africa and in Asia. The *Filicium* forest is adjacent to species rich forest at the same elevation (Lovett *et al.* 1997). The *Filicium* forest plots are significantly less diverse than the other plots (mean species per plot = 3 ± 1.5 , two-tailed t-test, $P < 0.0001$). Although the area is now not cultivated, parts of the *Filicium* forest are on places that have been cultivated in living memory. Other parts of the *Filicium* dominated forest are not so recently disturbed, with some *Filicium* trees in the plots up to 95 cm dbh. There are no Eastern Arc endemic tree species in the *Filicium* plots.

In another Southern Udzungwa forest at Mufindi, three plots in montane forest (1860–1870 m elevation) growing over old cultivation as evidenced by the remains of an undulating ridge and furrow system (Greenway 1973), also have significantly fewer species than other Eastern Arc plots (mean number of species in Mufindi plots = 5.3 ± 0.56 , two-tailed t-test, $P = 0.005$). The age of forest regeneration on cultivation at Mufindi has not been dated, but is beyond local memory. A marked qualitative difference between the Mufindi forests and other Eastern Arc montane forests can be demonstrated by pooling the three Mufindi plots to create a 60 tree sample and comparing them with three pooled plots from similar elevations elsewhere in the Eastern Arc. Data for the West Usambara, Southern Nguru and Northern Udzungwa were obtained by taking a random sample of three montane forest plots obtained from the same forest location on each mountain at as near an elevation as possible to the Mufindi plots. Plot elevations (m asl) are: West Usambara 1890, 1850, 1850; Southern Nguru 1480, 1500, 1560; Northern Udzungwa 1650, 1670, 1670; and Southern Udzungwa 1860, 1860, 1870. There are no Eastern Arc endemic tree species in the Mufindi plots compared to 20–30% of species from three other areas being Eastern Arc endemics (Table 2). With the *Juniperus*, *Filicium* and Mufindi plots excluded from the data pool the mean number of species per plot rises to 9.4 ± 2.3 ($n = 352$, mode = 10, median = 10, kurtosis = -0.28 , skewness = -0.07) and there is no correlation between plot species richness and elevation ($r^2 = 0.005$, $P = 0.18$).

In summary, the additional data included here support the observation that

Table 2. Comparison of numbers of species and endemism in samples of 60 trees from four montane forests in the Eastern Arc mountains of Tanzania. The 60-tree sample was obtained by combining three 20-tree plots.

	Species	Endemics
West Usambara	26	5
Southern Nguru	21	4
Northern Udzungwa	20	6
Southern Udzungwa	9	0

species richness in the Eastern Arc forests of Tanzania, measured as number of species in a sample of 20 trees ≥ 20 cm dbh, does not decline with elevation. Neither does the number of species per plot appear to be related to the richness of the potential pool of species at different elevations. As elevation is closely correlated with temperature, it can be assumed that plot species richness is independent of temperature. The driest forest type is less diverse than most of the other moist forests. This may be a function of precipitation or another factor, such as fire, which is associated with forests growing in low, seasonal rainfall. Forest regenerating on formerly cultivated ground has a comparatively low diversity and no endemic species.

ACKNOWLEDGEMENTS

I gratefully acknowledge permission from the Tanzania Commission for Science and Technology to conduct research in Tanzania, to Dr Alan Hamilton for use of data from the East Usambara mountains, and to Dr John B. Hall for use of data from Mazumbai in the West Usambara mountains. Comments on an earlier draft of the paper were provided by Luis Daniel Llambi Cartaya and two reviewers.

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